Title: Low levels of artificial light at night strengthen top-down control in insect food web

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SUMMARY

Artificial light has transformed the nighttime environment of large areas of the earth, with 88% of Europe and almost 50% of the United States experiencing light-polluted night skies [1]. The consequences for ecosystems range from exposure to high light intensities in the vicinity of direct light sources to the very widespread but lower lighting levels further away [2]. While it is known that species exhibit a range of physiological and behavioural responses to artificial nighttime lighting [e.g., 3, 4, 5], there is a need to gain a mechanistic understanding of whole ecological community impacts [6, 7], especially to different light intensities. Using a mesocosm field experiment with insect communities, we determined the impact of intensities of artificial light ranging from 0.1 to 100 lux on different trophic levels and interactions between species. Strikingly, we found the strongest impact at low levels of artificial lighting (0.1 to 5 lux), which led to a 1.8 times overall reduction in aphid densities. Mechanistically, artificial light at night increased the efficiency of parasitoid wasps in attacking aphids, with twice the parasitism rate under low light levels compared to unlit controls. However at higher light levels, parasitoid wasps spent longer away from the aphid host plants, diminishing this increased efficiency. Therefore aphids reached higher densities under increased light intensity as compared to low levels of lighting where they were limited by higher parasitoid efficiency. Our study highlights the importance of different intensities of artificial light in driving the strength of species interactions and ecosystem functions.

Keywords aphids, food webs, light pollution, parasitism rate, parasitoids

RESULTS AND DISCUSSION

We assembled replicate plant-aphid-parasitoid communities (see food web in Figure 1 F) in 48 mesocosms in the field and exposed them to different intensities of artificial light at night, ranging from 0.1 to 100 lux, for 10 aphid generations. To understand the mechanisms behind the

46 impacts of artificial light, we complemented the field experiment with small-scale experiments
47 under more controlled conditions.
48 In the field experiment, we found that low levels of artificial light at night (0.1 to 5 lux),
49 representing severe skyglow or direct light effects away from the immediate vicinity of typical
50 streetlight sources, had a strong impact on insect communities. The overall abundance of all three
51 aphid species feeding on bean plants (*M. viciae*, *A. pisum*, *A. fabae*) was reduced by 45.5 % under
52 low lighting levels in comparison to the control treatment with natural light levels (Figure 1;
53 treatments 0.1 lux ($t = -3.87$, $p = 0.0005$), 1 lux ($t = -2.57$, $p = 0.0147$) and 5 lux ($t = -2.75$, $p =$
54 0.0095), $df = 7,35$) whilst the higher levels of lighting (more typical of the immediate vicinity of
55 streetlights and more intense forms of lighting, such as that used in sports stadia and around
56 industrial installations) did not affect their densities ($p > 0.1$). The marked impact of low level
57 lighting on aphid numbers was driven by a 56.2% decline of the most abundant aphid species (*M.*
58 *viciae*) in 0.1, 1 and 5 lux treatments, compared to the control (Figure 1; treatments 0.1 lux ($t = -$
59 2.97, $p = 0.0053$), 1 lux ($t = -1.95$, $p = 0.0587$) and 5 lux ($t = -3.11$, $p = 0.0037$), $df = 7,35$). The
60 aphid *A. pisum* responded to light treatments with a similar trend to that of *M. viciae*, though this
61 pattern was not statistically significant compared to the control (overall treatment effect, $\chi^2 = 5.90$,
62 $df = 7$, $p = 0.5511$). The aphid *A. fabae* had a less predictable response to the treatments, with a
63 negative effect at 10 lux as compared to the control (Figure 1, $df = 7,35$, $t = -2.26$, $p = 0.0304$), and
64 a trend to higher densities in the 5 and 100 lux treatments. The grain aphid *S. avenae* feeding on
65 barley plants did not respond to the treatments (overall treatment effect, $\chi^2 = 2.10$, $df = 7$, $p =$
66 0.9541).
67 While we found a strong overall decline in aphid densities under low levels of light
68 compared to control conditions without light, aphid abundance increased from treatments with low
69 lighting to medium and high lighting levels, showing that the negative impact on aphids was
70 alleviated under higher intensity light treatments. Increasing light intensity (including all lit
71 treatments from 0.1 to 100 lux) had a positive effect on overall bean aphid numbers (Figure 1; df =

72 1,35, t = 2.65, p = 0.0119, with the model explaining 40% (conditional R^2) and the fixed effect
73 explaining 10% of the variation (marginal R^2)).
74 To explain the responses of the aphids it is necessary to look at the impact of the artificial
75 light treatments on their resource (the plants), as well as on their top-down control through
76 parasitoids. To test for the impact of light intensity (0, 0.1, 5, 20, 100 lux) on bean plant biomass we
77 conducted an additional experiment under controlled environmental conditions in a greenhouse in
78 the absence of aphids on plants. This revealed a positive correlation between light intensity and
79 plant biomass (Figure 2, df=1,23, t = 2.23, p = 0.0357). We found a similar trend in the plant
80 biomass data from the field experiment - where aphids were also present - but only in the 20 lux
81 treatment with significantly higher plant biomass than in the control (Figure S2, overall treatment
82 effect: $\chi^2 = 16.56$, df = 7, p = 0.0205). The biomass of barley showed no response in the field
83 experiment (Figure S2; overall treatment effect: $\chi^2 = 12.70$, df = 7, p =0.080). In sum, artificial light
84 at night, at least at higher levels has the potential to increase plant biomass, most likely through an
85 increased photosynthesis rate of plants leading to a positive bottom-up effect [8, 9], but this effect is
86 variable between species.
87 The parasitism rate of *A. megourae* attacking the aphid *M. viciae* in the field experiment
88 increased from 5% in the unlit control treatments to 10% in low light treatments (Figure 3 B, z =
89 2.910, p = 0.0036). The parasitism rate of neither of the other host-specific parasitoids, *A. ervi* and
90 *L. fabarum*, responded significantly to light treatments, but that of the latter showed a similar trend
91 to *A. megourae* (Figure 3, C & D). A two-fold increase in parasitism rate is a strong response,
92 especially over multiple generations, and can explain the observed effects of low lighting treatments
93 on aphid numbers. We found a strong decline in the overall parasitism rate (including all parasitoid
94 species) from a low to high level of nighttime lighting (Figure 3 A; linear regression between light
95 intensity and parasitism rate, z = -2.656, p = 0.0079).
96 The strong dependence of the strength of host-parasitoid interactions on artificial light
97 intensities in a field experiment under natural conditions is an important result and worthy of further

98 examination. We first compared the functional response of *A. megourae* under control conditions to
99 medium light levels (20 lux). The relationship between host density and the number of successful
100 attacks by *A. megourae* can be described by a type 2 functional response (Figure 4 A). The fitted
101 curve for the light treatment showed that parasitoid attacks saturated at a much higher level than in
102 the control, demonstrating that the parasitoids can attack more aphids in the 20 lux light treatment -
103 almost doubling attack rate under high host density situations (Figure 4 A). To test whether this
104 effect could explain the increased parasitism rate in the field experiment under low level lighting,
105 we then compared the number of successful attacks by *A. megourae* in control conditions to low
106 intensity (1 lux) and medium intensity (20 lux) treatments (Figure 4 B). This revealed that the
107 number of attacks increased significantly in the 1 lux treatment ($t = 3.17$, $p = 0.0053$, $df = 2,18$) and
108 marginally not significantly under 20 lux ($t = 2.07$, $p = 0.0536$, $df = 2,18$). These results indicate
109 that the activity of these parasitoids is strongly influenced by photoperiod [10]. We then showed
110 that this is indeed the case for the parasitoid *A. megourae*, with the vast majority of parasitoid
111 attacks happening during the day in a 12:12 day:night regime that included no artificial light at
112 night. Parasitism rate was 18 % during daylight, dropping to 2.5 % during dark hours (Figure S3, z
113 $= 7.294$, $p < 0.0001$); this species responds more strongly to photoperiod than has previously been
114 shown for the parasitoid *A. ervi* [11], explaining the stronger response to artificial light in the field
115 experiment. Artificial light at night thus extends the time budget of day-active parasitoids and
116 increases their ability to control aphid populations even at very low intensities of artificial light.
117 This usage of the so-called “nighttime niche” appears to be more widespread with evidence from
118 increased predation rates in ladybirds [12] and changed feeding habits of lizards [13] and birds [14].
119 However, the overall decline in parasitism rate with increasing light levels suggests that this niche
120 is strongly dependent on light intensity as the parasitoids are more efficient under low level
121 lighting. We tested therefore for the behavioural response of *A. megourae* parasitoids to different
122 light intensities in a setting with a mesocosm that contained a plant with 100 aphids. We found a
123 strong negative linear relationship between the proportion of female parasitoids that stayed on the

plant and light intensity (Figure 4 C, $t = -4.51$, $p < 0.001$, $df = 1,13$). Therefore at higher light levels the majority of parasitoids leave the plants with aphids, explaining why the parasitism rate is so strongly dependent on the level of light and the parasitoids most efficient at low light levels.

Overall, despite a potential bottom up effect through increased plant biomass providing more resources for aphids under higher light intensities, we show that the interaction between the aphids and parasitoids is the critical driver for the observed responses in the field experiment. Higher aphid densities were strongly associated with lower parasitism rates under control and high light treatments. Our experiment demonstrates that different intensities of artificial light at night change species interactions and food web dynamics in insect communities. As species interactions are an important building block of ecological communities this can have far reaching consequences for community stability and ecosystem functions. As demonstrated for other environmental stressors, some species respond while others remain unaffected. In our communities, the most abundant species responded, thereby driving the whole community response, and because species are interconnected in food webs even single species responses can drive whole community changes [15].

Host-parasitoid interactions are one of the most common food web interactions in terrestrial ecosystems [16], both natural and agricultural. The mechanisms demonstrated in our experimental communities therefore have major implications for ecosystems exposed to artificial light at night. The 'broad spectrum' white' lights used are typical of those being installed widely across the world for streetlighting and other outdoor purposes, particularly as the economic benefits associated with light-emitting diode (LED) technologies are exploited [17]; our findings may not be relevant to spectra more commonly associated with older lighting types, such as narrow spectrum low pressure sodium lamps. The surprisingly strong community response to low level artificial light is of major concern, because such light intensities are very widespread, and becoming more so with the continued spread in the extent of artificial lighting at 2 % per annum [18].

Our study further demonstrates that it is important to consider that the impacts of artificial light at night are strongly light intensity dependent and within a community context not necessarily possible to predict from single species responses. Prediction of the community response requires knowledge of major pathways, such as the balance between bottom-up and top-down effects. Species interactions are central to understanding the impact of artificial light at night on ecological communities and any resultant effects on ecosystem functions and stability.

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AUTHOR CONTRIBUTIONS

K.J.G. and F.J.F.v.V. conceived the project. K.J.G., F.J.F.v.V. and D.S. designed the experiments. D.S., R.K. and D.C. carried out the experiments. D.S. analyzed the data and wrote the first draft of the manuscript. All authors contributed to the manuscript. K.J.G. and F.J.F.v.V. acquired the funding for the work.

DECLARATION OF INTEREST

The authors declare no competing interests.

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MAIN FIGURE TITLES AND LEGENDS

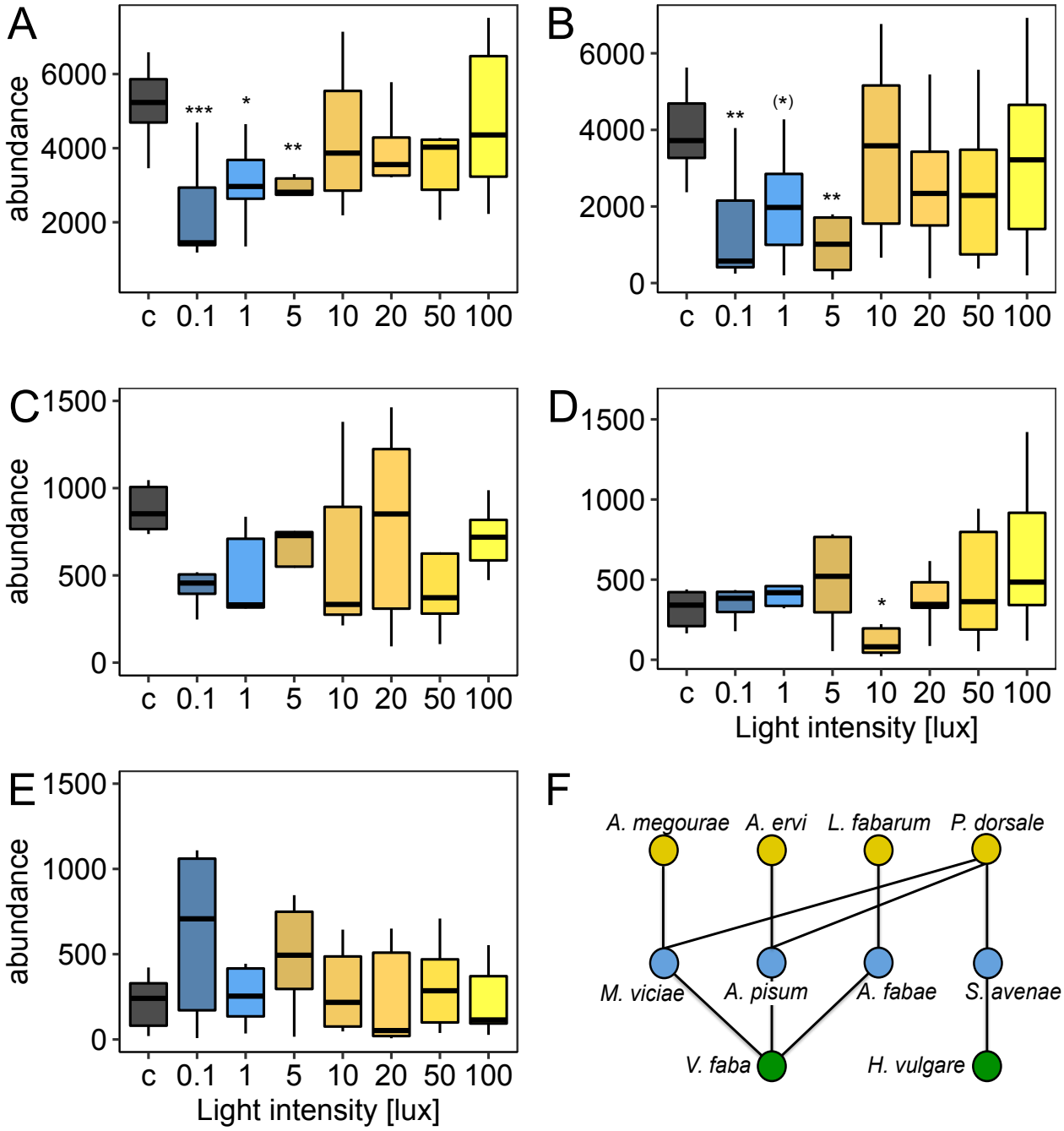


Figure 1. Aphid densities in the field experiment.

Boxplots presenting the median, and the lower and upper quartiles 25% and 75% of cumulative aphid densities for (A) all three aphids on *V. faba*, (B) *M. viciae*, (C) *A. pisum*, (D) *A. fabae* and (E) *S. avenae*, in mesocosms without light treatments (c = control) and in different treatments with increased light intensities at night (0.1, 1, 5, 10, 20, 50 & 100 lux). Each treatment was replicated 6 times. Statistical significance levels for comparison to the control treatment: (*) p=0.05, *p<0.05,

** p<0.01, *** p<0.001. (F) Food web structure of the experimental insect communities, with two plant species: broad bean (*Vicia faba*) and barley (*Hordeum vulgare)*, with three aphid species on beans: *Aphis fabae*, *Acyrthosiphon pisum* and *Megoura viciae*. Each of the aphid species was attacked by a specialist parasitoid, these being *Lysiphlebus fabarum*, *Aphidius ervi* and *Aphidius megourae*, respectively. The grain aphid *Sitobion avenae* fed on barley. The generalist parasitoid *Praon dorsale* attacked the aphids *S. avenae*, *A. pisum*, and *M. viciae*. See Figure S1 for population dynamics.

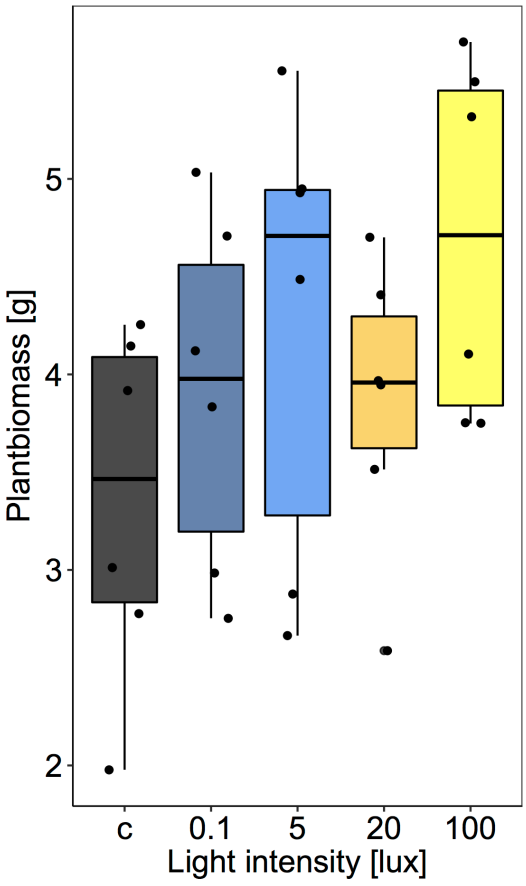


Figure 2. Plant biomass in greenhouse experiment without aphids.

V. faba plant biomass in control (black) and light treatments (0.1, 5, 20, 100 lux). Presented are the median, and the lower and upper quartiles 25% and 75% (based on 6 replicates). See Figure S2 for plant biomass in the field experiment.

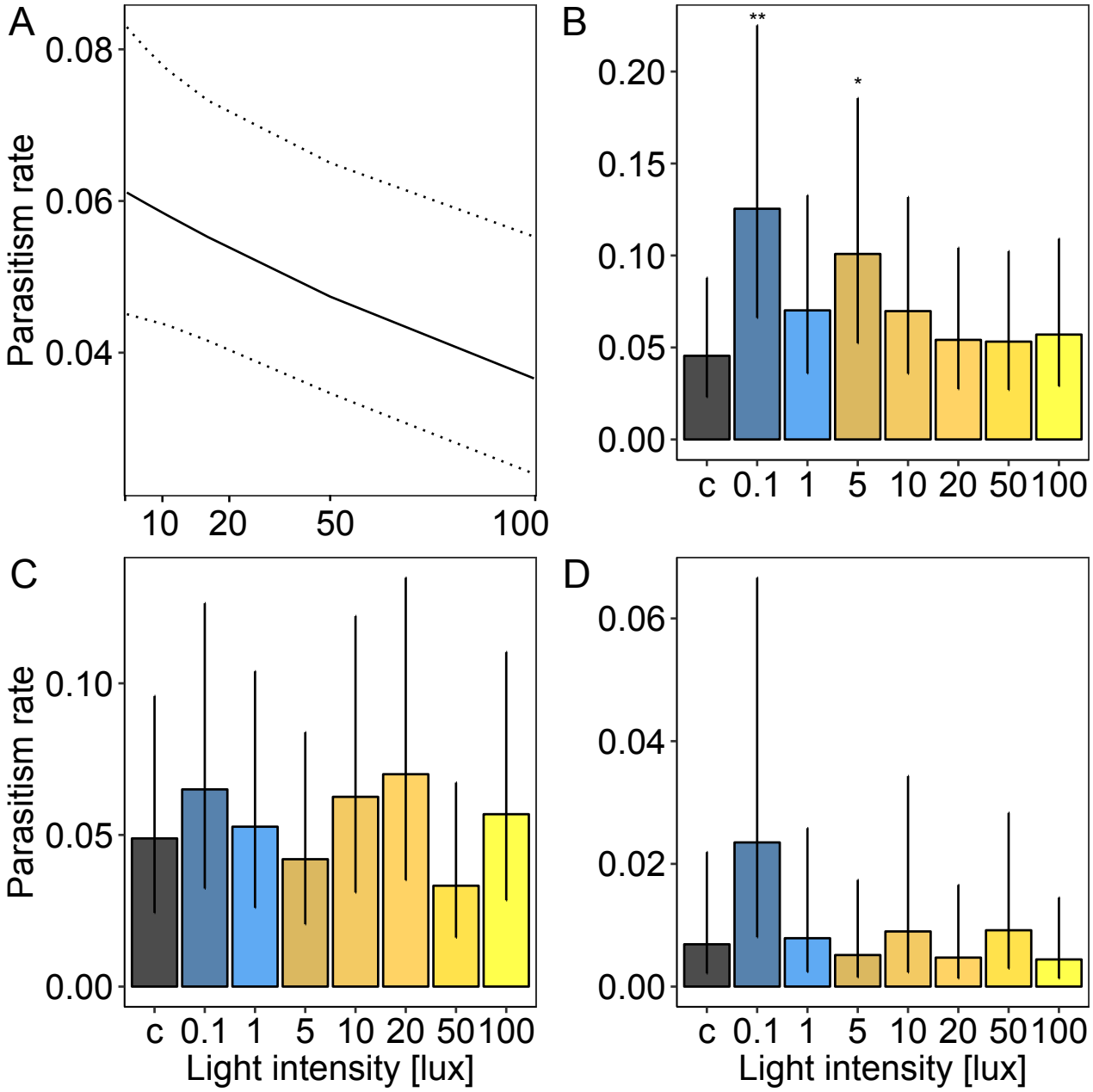
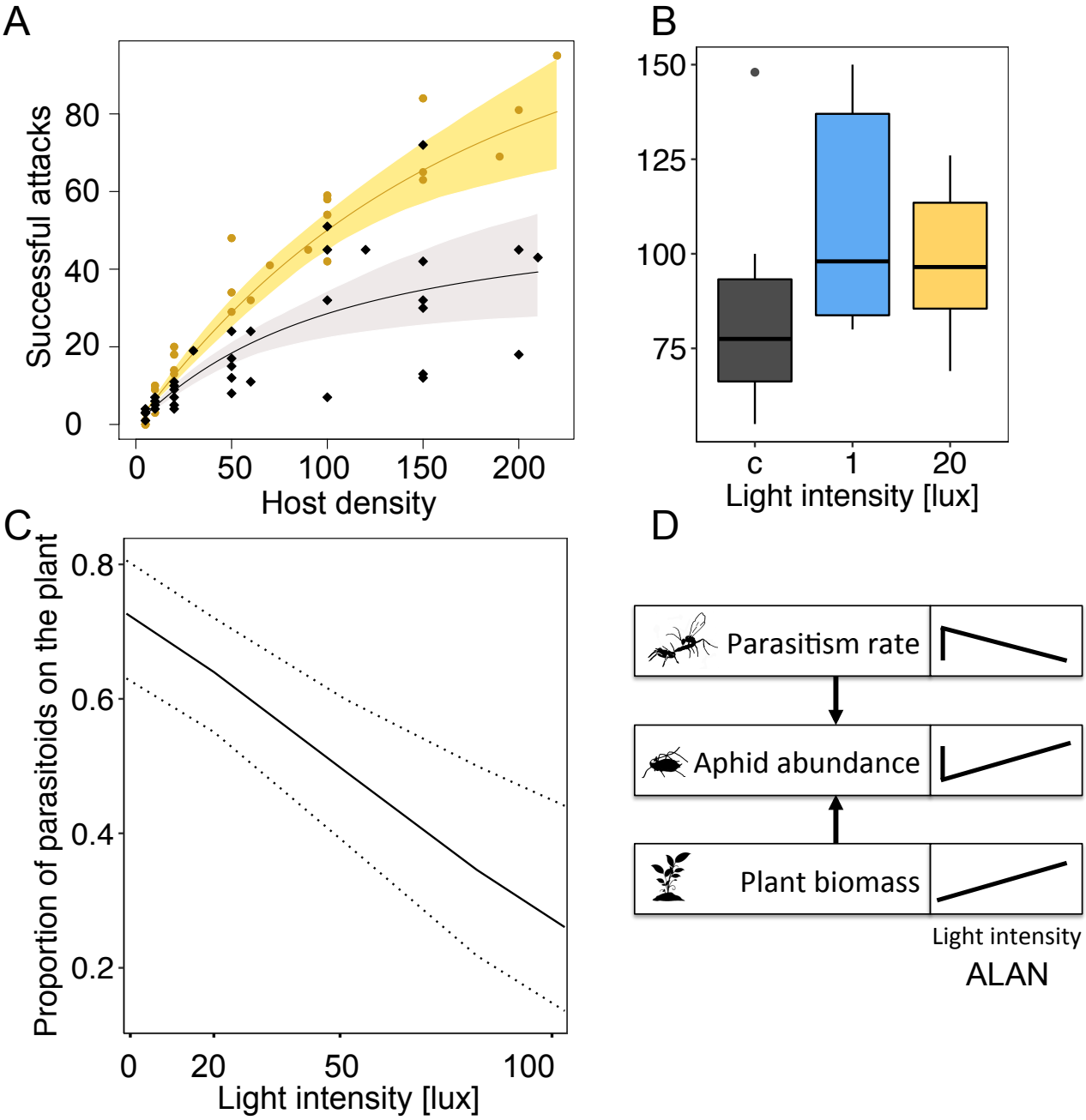


Figure 3. Parasitism rate in the field experiment.

(A) Mean and 95% CI for overall parasitism rate (all species) in relation to light intensity (0.1- 100 lux). Mean and 95% CI showing the parasitism rate for each of the parasitoid species (B) *A. megourae*, (C) *A. ervi* and (D) *L. fabarum* in control communities without artificial light at night (C) and communities exposed to different light intensities (0.1, 1, 5, 10, 20, 50 and 100 lux) at night (n= 6 for each treatment). The parasitism rate for the generalist parasitoid *P. dorsale* is not shown due to the low number of *Praon* aphid mummies detected in the experiment (see Figure S1H). Statistical significance level for comparison to the control treatment: *p<0.05, ** p<0.01.



265
266 **Figure 4. Parasitoid functional response and behaviour.**

267 (A) Functional response with a fitted Type 2 curve and 95% CI for the parasitoid *A. megourae*
268 attacking its host *M. viciae* under control (no light: black diamonds) and 20 lux at night (medium
269 light intensity: yellow circles). (B) Number of successful attacks in control, 1 and 20 lux treatment
270 (n =10, 8, 6 respectively) showing the median, and the lower and upper quartiles 25% and 75%, for
271 host density 140-180. (C) Proportion of *A. megourae* parasitoids staying in a plant with aphids
272 under different light intensities (measured for 0, 1, 5, 20 and 100 lux) (D) Overview of the

responses of different trophic levels to increasing ALAN intensities. See Figure S3 for attack rate during day and night.

STAR Methods

Contact for Reagent and Resource Sharing

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Dirk Sanders (d.sanders@exeter.ac.uk).

Experimental Model and Subject Details

The replicate experimental plant-insect communities (see Figure 1F) consisted of two plant species: broad bean (*Vicia faba*, L., var. the Sutton) and barley (*Hordeum vulgare* L.), with bean plants as a resource for three aphid species: (1) the black bean aphid *Aphis fabae* (Scopoli), (2) the pea aphid *Acyrthosiphon pisum* (Harris), and (3) the vetch aphid *Megoura viciae* (Buckton). Each of the aphid species was attacked by a specialist parasitoid, these being *Lysiphlebus fabarum* (Marshall), *Aphidius ervi* (Haliday), and *Aphidius megourae* (Stary), respectively. Barley plants were a resource for the grain aphid *Sitobion avenae* (Fabricius). These separate communities were linked by the generalist parasitoid *Praon dorsale* (Haliday), which attacked the aphids *S. avenae*, *A. pisum*, and *M. viciae*. Bean and barley seeds were bought from Kings Seeds, UK. Parasitoids were collected in the field (*L. fabarum* and *A. megourae, P. dorsale*) and received from Koppert, Netherlands (*A. ervi*). Aphids were from existing laboratory cultures *A. fabae* (Silwood Park, Berkshire, U.K), *A. pisum* (University of Oxford, UK) and *M. viciae* found on *Lathyrus pratensis* plants (Penryn, UK). Prior to the experiments, parasitoid and aphid cultures were kept in a controlled environment room at 20 °C, with a 16:8-h light:dark cycle.

Method Details

Field experiment

301 Experimental communities were established in 47.5 x 47.5 x 47.5 cm Bug Dorm mesocosms
302 (BugDorm-44545F Insect Rearing Cage, Megaview Science, Taiwan), which were secured with a
303 wooden frame and raised slightly above the surrounding vegetation, ensuring that all mesocosms
304 were at a similar height. Mesocosms were located 1.5 meters apart, and the vegetation around them
305 was mown fortnightly. The experiment was conducted in a contained field site at the University of
306 Exeter, Cornwall.
307 Light level treatments covered a range of light intensities; low light treatments (0.1, 1 and 5
308 lux) replicating city skyglow levels and levels away from the immediate vicinity of streetlights,
309 medium light treatments (10 and 20 lux) replicating levels in the immediate vicinity of streetlights,
310 and high light level treatments (50 and 100 lux) replicating more extreme lighting, for example
311 stadium or festival lighting. Each of the artificial light level treatments (0.1, 1, 5, 10, 20, 50 and 100
312 lux), and an unlit control were replicated 6 times and arranged in a randomized block design.
313 Lighting was located at the top of each mesocosm, and consisted of 36 watt 'Daylight White 5050
314 SMD LEDs' (Ledcentre.uk, London, cold white 5000 – 7000 Kelvin, see Figure S4 for spectrum).
315 The lighting levels were manipulated using a resistor to ensure the correct lux for each
316 treatment. Artificial lights were turned on only at night, by use of a dusk-dawn sensor, switching on
317 at 70 lux and off at 110 lux. Wooden barriers between the cages prevented spillover of light to
318 neighbouring mesocosms and mesocosms further away. Light levels were measured with a lux
319 meter (Delta OHM HD2102- 39 -V2.3 with Illuminance probe LP 471 PHOT/SICRAM module
320 measurement range starting at 0.01 lux with a resolution of 0.01 lux) in every mesocosm to confirm
321 the light levels per treatment. We compared treatment effects against a control treatment without
322 additional light but exposed to the varying influence of moonlight and very low levels of skyglow
323 as there were no direct light sources in the vicinity of the field site. This means the control is not a
324 entirely dark control but a natural nighttime light (as would be experienced in the absence of
325 streetlights) to which each treatment added the artificial light at a certain intensity. Field
326 experiments are important because they indeed include the natural variation as experienced by

natural communities but under more controlled conditions. The field site does experience low levels of artificial light at night through skyglow (as would be the case throughout much of Europe [1]), but readings from a Sky Quality Meter regularly reach values of 21 $mag_{SQM}/arcsec^2$ (lower levels occur, as would be expected, under moonlight and clouds), which compares favourably with what has been assumed to be a natural radiance of 21.6 $mag_{SQM}/arcsec^2$ [19]; note that higher values of these units mean less illuminance.

The experiment was set up on 29th July 2016, with 3 pots of broad beans and 1 with barley plants placed in each mesocosm and then a week later completed to a total of 6 pots of broad beans and 2 pots of barley per mesocosm. Five individuals of each aphid species were placed on the appropriate plant species and left for 2 weeks to grow in numbers. At weeks 2 and 3, two mated female parasitoids of each species were released into each mesocosm. Each week, the two oldest plant pots from each tray were replaced with 2-week-old plants, while leaving the plant matter and all insects in the mesocosm. This replicates the natural behaviour of aphid colonies, which typically show cycles of dispersal to fresh host plants.

From week 1 until the termination of the experiment after 9 weeks, all species on half of the plants were counted on a weekly basis. If no individuals of a particular species were found in a particular replicate, the entire mesocosm was checked to confirm presence or absence.

Plant biomass without aphids

We used 5 different light treatments to test for the effect of artificial light on plant biomass, in the absence of aphids: an unlit control, 0.1, 5, 20, and 100 lux. Each of the light treatments was replicated 6 times and arranged in a randomized block design. For each replicate a single 2 week old bean plant was placed in a 47.5 x 47.5 x 47.5 cm Bug Dorm cage, in a greenhouse with a 16: 8 hours light: dark period. The experiment ran for 3 weeks, at which point the plants were washed clean of soil, the aboveground and belowground parts separated, and dried at 50^{o}C for 48 hours. They were then weighed to within 0.001 gram.

353

354 *Parasitoid functional response and attack rate*

355 Third instar *M. viciae* aphid individuals were set onto 2 week old plants at densities varying from 5
356 to 200, with each plant placed in a 47.5 x 47.5 x 47.5 cm Bug Dorm cage, in the contained field site
357 at the University of Exeter, Cornwall. One female *A. megourae* parasitoid was placed in each cage
358 for a 24-hour period, after which point it was removed. Aphids were then left for 2 weeks before all
359 mummies were counted. We used two treatments: unlit controls and artificial light at night at 20
360 lux. This experiment ran at the same time as the large field experiment.

361 We compared parasitoid attack rate between control (no light), 1 lux and 20 lux treatment. 1
362 female *A. megourae* parasitoid was released on a plant with 150 *M. viciae* aphids, and left for 24 h.
363 This was done in a controlled Temperature room at 20 degrees C and 16: 8 hours light: dark period.
364 Each treatment was replicated 6 times, and parasitoid mummies were counted after 2 weeks.

365

366 *Parasitoid activity*

367 To test for the behavioural response of parasitoids to different light intensities, 100 3rd instar *M.*
368 *viciae* aphids were placed on a 3 week old broad bean (*V. faba* plant) and allowed to settle in a
369 climate chamber with a 16:8 light: dark cycle for 24 hours. This infested plant was then placed in a
370 cage in complete darkness. Different light treatments were then applied over the top of the cage,
371 these being 0 (control) 1, 5, 20, and 100 lux, measureable at the height of the plant (in exactly the
372 same setting as for the field experiment). 20 mated female A. *megourae* parasitoids were then
373 released into the cage, and were left for one hour. After one hour the locations of the parasitoids (on
374 the or away from plant) were noted. Preliminary tests using the artificial light treatments along with
375 red lights showed that there was a period of 20 seconds for counting before the parasitoids changed
376 their location or activity after the counting light was put on.

377 To test for parasitoid attack rate during day and night, single broad bean plants were
378 infected with 60 3rd star *M. viciae* aphids per plant, and placed in a 20 x 20 x 40 cm cage

constructed of untreated wood and thrip netting. These aphids were left to settle for 1 day before being placed in incubators (Percival Model 1-30 vl) set to 18 degrees C with a 12:12 day night cycle and 75 % humidity. A single, mated female *A. megourae* parasitoid was placed in each cage, and left for 12 hours in either dark or light settings. After 12 hours the parasitoid was removed and placed in another cage, again with 60 3rd instar aphids and left for a further 12 hours at the opposite light treatment. After the removal of the parasitoid, each cage was placed in a controlled temperature room at 18 degrees and a 16:8 day night cycle for mummies to develop. After 2 weeks the number of mummies per cage was counted.

Quantification and statistical analysis

All data were analysed using the open source software R 3.3.2 [20].

Field experiment

The impact of light treatments on plant biomass and aphid populations in the field experiment was analysed with linear mixed effects models using the function lme from the package nlme [21]. We included treatment (with 8 levels) as a fixed factor, while block was included as a random factor. As response variables we used aphid cumulative numbers (for each of the species the sum of aphids counted per single mesocosm) and plant dry weight (separated for bean and barley plants). We also tested for a linear response of overall aphid numbers to increasing light intensity (0.1 to 100 lux).

Parasitism rate was analysed using generalised linear mixed models assuming a binomial error distribution and using the logit link function. The response variable was the bivariate variable containing 'cumulative parasitoid mummies of aphid species i' and 'cumulative abundance of alive aphids for species i', where 'i' can be the cumulative abundance or mummy number of *A. fabae*, *M. viciae*, or *A. pisum*. The parasitism rate of the generalist parasitoid *P. dorsale* was not analysed due to the low sample size. Block was included as a random factor, and to account for over-dispersion, an additional observation-level random factor was added. For this analysis we used the function

405 glmer from the package lme4 [22]. To obtain 95% credible intervals for the model predictions, we
406 used the R-package "effects" [23]. We also tested for a correlation between overall parasitism rate
407 in the community (including all parasitoid species) and light intensity (0.1 to 100 lux).
408
409 *Plant biomass without aphids*
410 The impact of light treatments on plant biomass in the absence of aphids was analysed with linear
411 mixed effects models using the function lme from the package nlme [21]. We included light
412 intensity (0, 0.1, 5, 20, 100 lux) as a continuous explanatory variable, while block was included as a
413 random factor. As response variable we used plant dry weight per single mesocosm.
414
415 *Parasitoid functional response*
416 The functional response curve for the parasitoid *A. megourae* attacking aphids under unlit control
417 conditions and the treatment with artificial light at night (20 lux) were fitted using the function
418 frair_fit and confidence intervals were estimated with frair_boot from the frair package [24].
419
420 *Parasitoid attack rate during light and dark period*
421 Parasitoid behaviour under different light intensities (0, 1, 5, 20, 100 lux) and parasitism rate in
422 dark and light periods were analysed using generalised linear models assuming a quasi-binomial
423 error distribution. The response was the bivariate variable containing 'parasitoids on the plant' and
424 'and parasitoids away from the plant' in the first and'*A. megourae* parasitoid mummies' and
425 'abundance of alive *M. viciae* aphids' for the latter analysis, which was analysed with treatment (12
426 h light or 12 h dark period) as explanatory. To obtain 95% credible intervals for the model
427 predictions we used the R-package "effects" [23].
428
429 **Key resource table (**see extra document)
430

Data and software availability

All data used in this study have been deposited at the Environmental Information Data Centre under the link XXXX.